THE CARABID FAUNA OF THE UPLAND OAK FOREST IN MICHIGAN: SURVEY AND ANALYSIS[1]

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Abstract

The carabid faunas of three sites in the upland oak forest in Michigan were sampled by pitfall traps, sticky board traps, malaise traps, pyrethrum spraying, and hand collecting. The various collecting methods permitted sampling of arboreal Lebiini present in the forest, as well as of non-resident immigrant species entering the upland oak forest. The three sites in this second growth forest differ in stage of succession. The more mature stands contain carabid faunas of greater diversity and decreased dominance. This is related to increased resources and increased heterogeneity in the mature stands, allowing greater interspecific competition and more species packing.

The insect community associated with oaks in the Manistee National Forest near Baldwin, Michigan has been the target of intensive study since 1973. Studies on the dynamics of the variable oak leaf caterpillar (*Heterocampa manteo* Doubleday: Notodontidae) and the red humped oakworm (*Symmerista cannicosta* Franclemont: Notodontidae) have elucidated the basic structure of the oak defoliator complex and related parasitoids (Surgeoner 1976). In addition, studies of the major predators in the upland oak forest have been made, with an intensive study of two lebiine carabids, *Pinacodera platicollis* Say and *Pinacodera limbata* Dejean (Mahar 1978).

With these data as a base, a survey of the carabid fauna of the upland oak forest was made in 1977. The survey characterized the carabid community of three plots which had been studied since 1973. This characterization provided information on the ecological requirements of carabids found associated with the oaks, elucidated the interactions within the complex of ground inhabiting predators, and correlated the diversity of the carabid fauna with the stage of succession of the upland oak forest.

Study site

The Manistee National Forest is composed of 1,358,500 ha in the northwest quadrant of Michigan's lower peninsula. The forest covers portions of counties and contains various floral communities. By far the most common type of habitat present is the upland oak forest. The trees in these areas are predominantly red oak (*Quercus rubra* L.) and white oak (*Quercus alba* L.), with red maple (*Acer rubrum* L.) and aspens (*Populus* spp.) of secondary mportance. The soil is a sandy loam, with a 5 to 10 cm horizon of organic matter created by leaf decomposition. This habitat is generally dry due to good drainage, and with varying closure of the canopy, xeric to mesic conditions exist on the forest floor.

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Our study was made at three sites in the red oak-white oak upland forest. The tree species composition was sampled using the quarter method as described by Curtis and Cottam (1950). The ground cover was characterized by the transect method, using 10 3-m transects in each site. One soil sample was taken at each site, and mechanical composition, pH, and percent organic matter were determined.[3]

The first site was located near Dublin, Michigan (Manistee Co. T21N, R14W, S.36) and was a scrub oak forest association, hereafter called Dublin (Dub). The predominant tree species was white oak, with red oak and trembling aspen (*Populus tremuloides* Michx.) of secondary importance (Table 1). Trees averaged 140.0 square cm basal area and were an average of 4.36 m apart. The canopy was open, with the ground receiving much sunlight and therefore exhibiting xeric conditions. Crabgrass (*Digitaria* sp.) was plentiful, with bracken (*Pteridium aquilinum* (L.)), sweet fern (*Comptonia perigrina* (L.)), and white oak seedlings comprising the major portion of the remaining ground cover. In addition, the open clearings of the Dublin site had abundant lichen cover.

The second site was located near Branch, Michigan (Lake Co., T18N, R14W, S.4) and will be called Branch Pole (BP). This area of the forest was more advanced successionally, with the canopy closed and trees of approximately the same age class present throughout the plot. White oak and red oak were of approximately equal importance, with red maple also present (Table 1). The trees were more closely spaced, though they averaged the same size as at Dublin. The variation in tree size was much less than at Dublin, and the canopy was closed. This was reflected in the flora of the forest floor. Sassafras seedlings (*Sassafras albidum* (Nutt.)) were dominant, with crabgrass, bracken, and blueberry (*Vaccinium* sp.) the secondary ground cover species. In addition, black cherry (*Prunus serotina* Ehrh.), white oak, and red maple seedlings were present.

The third, most mature site was also near Branch, Michigan (Lake Co., T18N, R14W, S.5), hereafter referred to as Branch Mature (BM). Like the other sites, red and white oak were the dominant tree species here; however, several other species were also found (Table 1). The trees were larger, averaging twice the basal area as at the other 2 sites. With maturity, tree density was less, permitting the emergence of a secondary canopy of sassafras, witch-hazel (*Hamamelis virginiana* L.), and dogwood (*Cornus* sp.). Thus, openings occurred in the canopy, but the ground was intermittently shaded by the understory. The ground cover was dominated by sassafras. Bracken, blueberry, and black cherry, witch-hazel, and red maple seedlings comprised the majority of the remaining ground cover. The topography at Branch Mature differed from Branch Pole. The area was on the north slope of a gently elevated ridge. Thus the soil was moister than at the level area of Branch Pole.

The soil composition of the three sites was nearly identical (Table 2), with all having a pH less than 5.0. The mechanical composition and percent organic matter were also very similar. Thus, any differences in forest

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[3] Soil Testing Service, Dept. Crops and Soil Science, Michigan State Univ., E. Lansing, MI 48824.

Table 1: Tree composition at three study plots. I.V. = importance value (Curtis and Cottam, 1950).

Dublin		Branch Pole		Branch Mature	
Tree Species	I.V.	Tree Species	I.V.	Tree Species	I.V.
Red Oak	83.7	Red Maple	15.0	Red Maple	35.0
White Oak	168.7	Red Oak	163.1	Red Oak	64.5
Trembling aspen	39.9	White Oak	122.0	White Oak	97.0
Choke cherry	7.7			Big-toothed Aspen	38.9
				Dogwood	12.3
				Witch hazel	20.7
				Sassafras	31.7
trees/hectare = 525.9		trees/hectare = 1327.9		trees/hectare = 734.6	
ave. basal area (cm^2)/tree = 140.0		ave. basal area (cm^2)/tree = 140.6		ave. basal area (cm^2)/tree = 280.6	
ave. dist. between trees(m) = 4.36		ave. dist. between trees(m) = 2.74		ave. dist. between trees(m) = 3.69	
basal area (cm^2)/hectare = 73,626		basal area (cm^2)/hectare = 186,703		basal area (cm^2)/hectare = 206,129	

Table 2: Soil characteristics at the three study plots.

Site	pH	%sand:%silt:%clay	% organic matter
Dublin	4.9	81.5:7.1:11.4	5.9
Branch Pole	4.6	80.5:8.5:11.0	4.4
Branch Mature	4.4	81.5:8.1:10.4	3.9

type between the three sites can be related primarily to drainage and the availability of water.

The use of the forest by man is the principal reason for its present condition. The virgin forest in this area was predominantly white pine (*Pinus strobus* L.). This was clearcut beginning about 1870. Cutting was completed by the mid 1890's. After clearcutting, the land was susceptible to fire, and it did burn several times (Elliot 1952). The fires removed the organic matter from the soil, requiring that secondary succession start from bare sandy soil. Because of this, the three sites can be considered part of a recently established community which includes oaks and associated insects that have colonized the burned areas during the past 100 years.

MATERIALS AND METHODS

The study of carabid population dynamics is nearly always done by using pitfall traps (Allen and Thompson 1977; Harris and Whitcomb 1971; Johnson *et al.* 1966). If used alone, this method suffers from 2 principal faults: 1) passive sampling as exemplified by pitfall traps monitors activity as well as abundance, and results must be interpreted in that context; and 2) many species are active much of the time in microhabitats other than the soil surface, and thus some species may appear very rare if other suitable sampling methods are not used. Therefore, to most fully survey the carabid fauna in the three plots, various sampling methods were used in addition to pitfall trapping. These methods could not be correlated quantitatively; however, this was of little concern, since each type of trapping method could sample different species or those whose habits do not allow capture by other means.

Plastic containers, with openings 11.5 cm in diameter, were used for pitfall traps. These were placed in holes cut with a golf hole cutter. Masonite covers 20 cm square supported by 3 large nails were used to exclude leaf litter and rainwater. The ground cover in the 3 plots was fairly sparse, with leaf litter comprising most of the organic matter immediately surrounding each trap. Only at Dub were some traps placed in areas of vegetation. Thus, major problems of dense vegetation described by Greenslade (1964) could be eliminated by removing leaf litter from around the traps. This enabled comparison of trap catches at the 3 sites, as the locomotory activity of the ground dwellers could not have been seriously hampered at any of the sites.

At each site, 2 replicates of 10 traps were set out in lines, with traps spaced approximately 10 m apart. The replicates were situated perpendicularly, with 20 m separating the 2 lines. The separate trap lines allowed the greatest surface area to be sampled using the least number of traps. The traps in these 6 primary replicates were filled to a depth of 1 to 2 cm with a 2:1 ethylene glycol:water mixture. The traps were set out 8.IV.1977 when snow cover was still present, and checked weekly from 15.IV until 14.X, with a final check made 27.X.

From 10.VII until 27.X, a second group of 60 pitfall traps was set out. Three parallel lines of 10 traps separated by 20 m were run at each of the BP and BM plots. These were live pitfalls, traps without covers or preservative. They were checked daily by JM during times of residence in Lake Co. These traps were not analyzed quantitatively, but they did give some valuable collecting records, as well as live adults and larvae for rearing.

To sample arboricolous and other flying carabids, sticky board traps were used. Two pieces of plywood 25 cm × 45 cm were slit halfway through at the middle and intersected, giving a trap with eight 25 cm × 22.5 cm vanes. The vanes were coated with a layer of Tack Trap.[4] The traps were hung by a rope from screw eyes set into larger oak trees, at heights of 1.5, 5, and 10 m, as far from the trunk as possible. In 1977, 2 sets of 3 traps were used per site, and they were checked weekly. In 1976, 8 sets of 3 traps were set out.

In 1976 and 1977, malaise traps were used to survey the flying insects at BP and BM. A ground level, 2 directional malaise trap was placed at BP, and checked weekly. A 2 directional aerial malaise was placed 10 m up the trunk of a white oak at BM and checked biweekly. In addition, ground level malaise traps were placed at all 3 sites in 1973 through 1975.

Pyrethrum spraying of selected trees at all 3 sites was carried out from 1974-1977. A back-pack sprayer was used to dispense an emulsifiable concentrate of pyrethrum from the top of a 40 foot long truck mounted ladder. Specimens collected were retrieved from a large nylon tarp placed under the tree.

Carabids were also sampled by hand collecting in the plots. This method was especially effective in spring and fall, as inactive overwintering immigrants in the plots were discovered.

After traps were sampled, all specimens were pinned and labelled. With several species, the condition of the ovaries was of concern. To study this, pinned female specimens were immersed in boiling water for about 10 minutes, after which the tissues were adequately reconstituted so that the presence of corpora lutea, and the status of the ovaries could be determined upon dissection.

Three indices were used to analyze the pitfall trap capture data: 1) the Shannon-Weaver index of diversity, H'(s); 2) the evenness coefficient, J; 3) the index of Simpson, or dominance value, C. The Shannon-Weaver index expresses the uncertainty of predicting the identity of a species when randomly drawing individuals from a community (Poole 1974). An increase in the number of species present, or an increase in the equality of abundance of the various species, increases the value of H'(s). The evenness coefficient expresses the equality of abundance of the various species in the community. Therefore, a higher value of J means species are present in more equal numbers. The dominance value, C, is strongly influenced by the one or two most common species, and so is an index expressing the degree of dominance of those species. Whittaker (1972) reviews the uses of each of these indices in the analysis of diversity.

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[4] Tack Trap®, Animal Repellants, Inc., 1016 Everee Inn Road, P.O. Box 999, Griffin, GA 30224.

To aid in the visualization of species interactions in the three habitats, dominance-diversity curves were constructed using percent biomass contributed by each species sampled by pitfall trapping. To determine the biomass of each species trapped, 10 individuals of each species were weighed to the nearest .001 gm using a single pan analytical balance. Specimens were not oven dried, but had been collected and pinned at least 4 months before weighing, and were quite brittle. On those species of which less than 10 specimens were trapped, as many specimens as possible were weighed.

RESULTS

A total of 37 species of Carabidae was collected in the 3 study plots. Most were trapped by the pitfall method (Table 3); however, some species were captured by other means (Table 4). The most carabids were trapped at Branch Mature (BM), the least at Dublin (Dub). Both BM and Branch Pole (BP) had similar numbers of species present, whereas Dub was generally less diverse.

Table 3: Total captures for the three sites using pitfall traps, and number of species captured at each site.

Species	wings	Dublin	B.P.	B.M.
Cicindela sexguttata Fabr.	+	0	1	0
Sphaeroderus lecontei Dej.	-	3	10	5
Carabus limbatus Say	-	128	67	55
Carabus serratus Say	-	6	4	4
Carabus sylvosus Say	-	1	9	2
Calosoma calidum Fabr.	+	4	1	0
Calosoma frigidum Kirby	+	0	7	2
Notiophilus semistriatus Say	±	6(-)	0	1(+)
Notiophilus novemstriatus Lec.	+	1	0	0
Bembidion transparens Gebler	+	0	0	1
Myas coracinus Say	-	8	14	30
Myas cyanescens Dej.	-	0	0	3
Pterostichus adoxus Say	-	0	16	6
Pterostichus chalcites Say	+	0	1	0
Pterostichus pensylvanicus Lec.	±	24	342	299
Pterostichus mutus Say	+	0	31	179
Calathus gregarius Say	-	83	139	297
Synuchus impunctatus Say	-	4	33	95
Harpalus laticeps Lec.	+	0	2	0
Harpalus erythropus Dej.	+	1	0	0
Episcopellus autumnalis Say	+	0	0	1
Badister reflexus Lec.	+	0	0	1
Dicaelus purpuratus Bonelli	-	1	0	0
Pinacodera limbata Dej.	+	3	9	24
Pinacodera platicollis Say	+	1	18	23
Metabletus americanus Dej.	±	5	4	3
Cymindis neglecta Haldeman	-	1	0	0
Total trapped		280	708	1031
# spp. in pitfalls		17	18	19
Total # spp.		18	24	24

Table 4. Species collected by means other than pitfall traps, 1974-1977: dates (number of specimens); X = numerous captures with dates in results.

Species	wings	method	Dublin	B.P.	B.M.
Cicindela sexguttata Fabr.	+	malaise	-	20 V 77(4)	-
Clivina bipustulata Fabr.	+	hand	-	24 IX 77(1)	-
Dyschirius sp.	+	pyrethrum spray	-	1 VI 77(1)	-
Agonum tenue Lec.	+	hand	-	-	8 IV 77(1)
Gynandropus hylacis Dej.	+	pyrethrum spray	-	10 VI 76(1)	-
Episcopellis autumnalis Say	+	sticky board	-	-	1 VII 76(1)
Bradycellus kirbyi Horn	+	malaise	-	-	24 VI 74(1)
Lebia viridis Say	+	malaise, spray	-	20 V 77(1)	-
Lebia bivittata Fabr.	+	hand	-	23 X 77(1)	-
Dromius piceus Dej.	+	sticky board, pyrethrum spray	X	X	X
Plochionus timidus Hald.	+	sticky board	-	-	X
Pinacodera platicollis Say	+	sticky board, hand, malaise, spray	X	X	X
Pinacodera limbata Dej.	+	sticky board, hand, Malaise, spray	X	X	X
Cymindis cribricollis Dej.	+	hand	-	-	7,17 VIII 77(1,1)

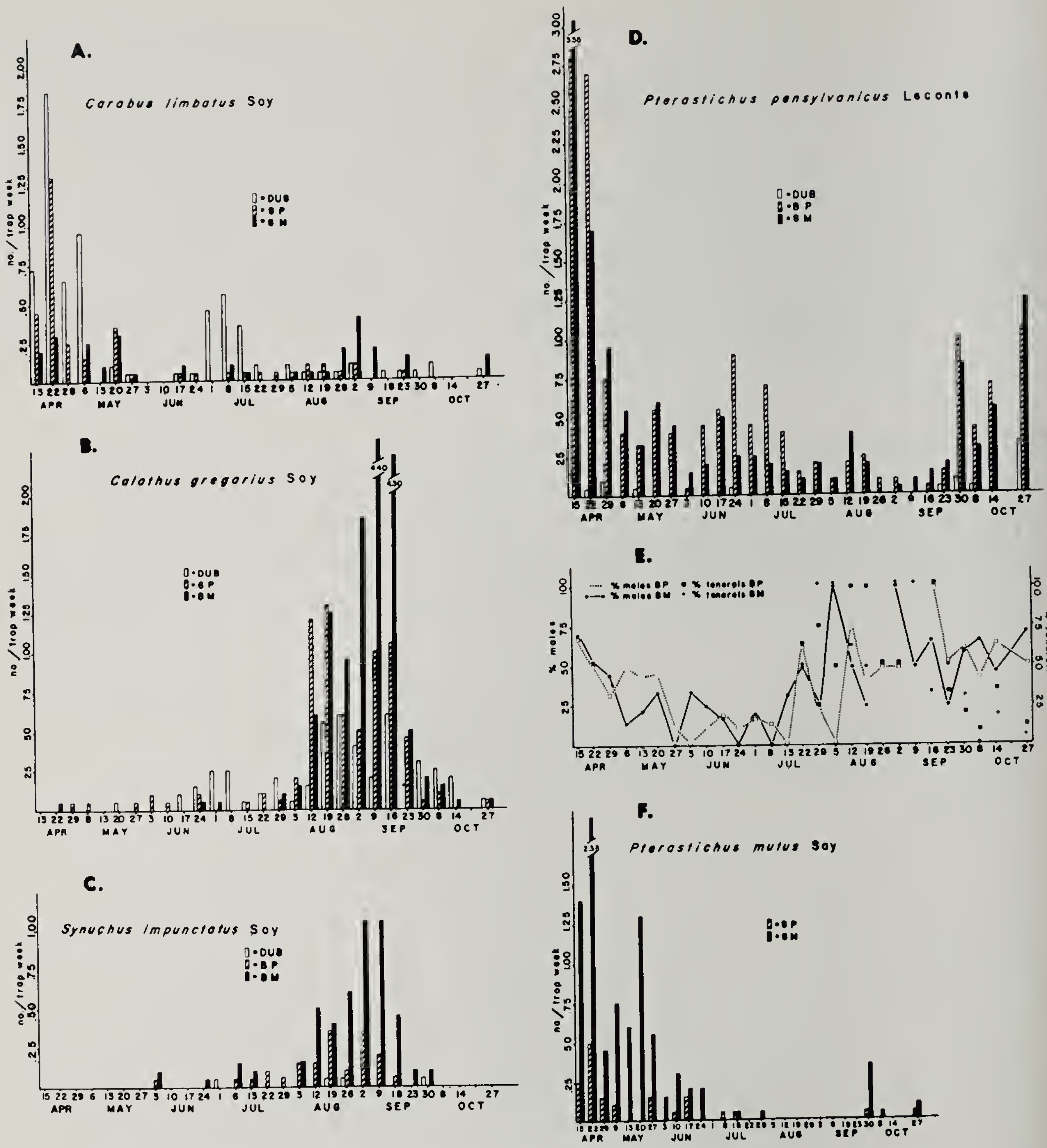

Figure 1, Weekly capture results for pitfall trapping: A. *Carabus limbatus* Say; B. *Calathus gregarius* Say; C. *Synuchus impunctatus* Say; D. *Pterostichus pensylvanicus* Leconte; E. percent males and percent tenerals trapped for *Pterostichus pensylvanicus*; F. *Pterostichus mutus* Say.

The pitfall trap captures of the 5 most commonly trapped species (Figure 1), show the two basic types of life cycles for the Carabidae. *Carabus limbatus* Say, *Pterostichus pensylvanicus* Leconte, and *P. mutus* Say overwinter as adults, whereas *Calathus gregarius* Say and *Synuchus impunctatus* Say overwinter chiefly as larvae.

Calosoma frigidum Kirby adults were trapped on 20, 27.V. Relatively large numbers of larvae were captured in pitfall traps. At BP, first instar larvae were trapped 27.V; 10, 17.VI; and second instar larvae were trapped 1, 7 (2 larvae), 15.VII. One third instar larva was trapped at BM, 24.VI.

Only one specimen of *Episcopellus autumnalis* Say was taken in the ethylene glycol pitfall traps, this a teneral caught the week of 2.IX at BM.

Table 5: Sticky board and pitfall trap catches for 3 species of arboreal lebiine carabids, male:female captures.

Species	Sticky board traps 1976	Sticky board traps 1977	Pitfall traps 1977
D. piceus	5:5	6:3	-
P. platicollis	4:7	1:1	8:34
P. limbata	57:35	23:11	11:25

Other captures were made at BM: 2 taken by hand the weeks of 15, 20.IV; 3 specimens live pitfall trapped the week of 29.VII; a total of 8 live trapped the weeks of 2, 9.IX. In addition, one specimen was trapped by sticky board at BM, 1.VII.1976. The sites of the live pitfall traps that collected the 11 *E. autumnalis* were isolated from each other, with only 2 adjacent traps on each of 2 lines collecting the adults.

Four species of lebiine carabids are present in the oak forest for which pitfall trapping gave partial or inadequate life history data. *Dromius piceus* Dejean was taken in all 3 plots (Table 4). No specimens were trapped in pitfalls, but numbers were trapped with sticky board traps (Table 5). In 1977, adults were captured the weeks of 13, 20.V; 1, 8, 15.VII. In 1975, a pyrethrum spraying of an oak at Dub, 8.IX, yielded 8 specimens, one of which was teneral. One pupa was collected under a loose bark flap, 6 m up the trunk of a white oak at Branch, MI; 27.VIII.1976.

Plochionus timidus Haldeman is another lebiine present in the oak forest, and 6 specimens were trapped with sticky boards at BM in 1976: 2 trapped the week of 10.VII; 1 trapped the week of 27.VII; 3 trapped the week of 8.IX.

Two other species of Lebiini commonly trapped were *Pinacodera platicollis* Say and *Pinacodera limbata* Dejean. *P. platicollis* is found at all 3 sites, though it is more common in the closed stands. Captures were made in pitfall traps the weeks of 15, 22.IV; 6, 13, 20.V; 2, 16, 23, 30.IX; 7, 14, 27.X. Sticky board captures of adults are limited (Table 5), principally because of cool weather when the adults are active. However, this species is active both on the ground and in the trees.

Pinacodera limbata is also active in the trees and on the ground. Pitfall trap captures were made the weeks of 1, 8, 15, 22, 29.VII; 19, 26.VIII; 2, 16, 23.IX; 7, 27.X. Females were more commonly trapped in the pitfall traps (Table 5). In 1977, adults were captured on sticky board traps the weeks of 13, 20.V; 3, 17, 24.VI; 1, 8, 15, 22, 29.VII; 5, 12, 19, 26.VIII. In both 1976 and 1977, many more males than females were trapped via sticky board. The larvae are terrestrial, and were captured in live pitfall traps at BP on 2, 4, 21, 31.VIII; and 22.X.

DISCUSSION

Analysis of Capture Data

Although no experiments were run specifically to test hypotheses related to habitat preference or bionomics of the carabids, data from the faunal survey illustrate certain points.

Carabus limbatus was present in all plots, with most specimens trapped at Dub. The adults overwinter, with adult activity chiefly in spring (Figure 1A). At Dub there was a second period of activity in July. This was probably due to activity of newly emerged adults, as well as increased activity of old adults. Of the 7 females trapped the week of 8.VII at Dub, 3 were virgins, 3 had degenerate ovaries with corpora lutea present indicating they had oviposited, and one female had corpora lutea with one partially developed egg present. Thus, probably environmental as well as intrinsic factors accounted for the increase in activity. There was no different temporal distribution of male and female activity, with females generally more active throughout the season.

Some carabid species will aggregate, especially in habitats offering few areas of shelter relative to the number of beetles present (Greenslade 1963). The captures of *C. limbatus* at Dublin in spring appear to illustrate such aggregation. Three of the first 4 weeks exhibit captures which are concentrated in 3 traps of one of the 2 lines. If we assume that the proximity of an overwintering spot to a pitfall trap has a direct relationship to the probability of capture when spring activity commences, it appears that *C. limbatus* exhibited a contagious distribution when trapping was started (Table 6). After 6 May, all captures at Dub were randomly distributed. Captures at other plots, and with other species did not exhibit an aggregated distribution. The captures of new adults in July suggest that they are active for a number of weeks before ceasing activity prior to overwintering. Thus, in the xeric habitat at Dub, it appears that *C. limbatus* is restricted in its choice of sites in which to enter dormancy, and must aggregate when activity ceases.

Notiophilus semistriatus Say was pitfall trapped at Dub and at BM. All 6 specimens trapped at Dub were brachypterous, indicating that the species is a resident there. The one specimen trapped at BM was macropterous, and may represent a colonist coming into the closed canopy forest.

Pterostichus pensylvanicus adult activity was concentrated in early spring (Figure 1D). Males were more commonly trapped in April and in late September through October. Between these periods females were more commonly trapped (Figure 1E). Thus, it appears that mating here occurs

Table 6: Type of distribution of *Carabus limbatus* at Dublin plot, 1977. Chi-squared test for agreement with a Poisson series (Elliott, 1971).

week	X^2	distribution
15 IV	69.40	contagious
22 IV	110.44	contagious
29 IV	18.32	random
6 V	42.60	contagious
13 V	-	-
20 V	16.20	random

both in spring and fall as found by Barlow (1970) and Goulet (1974). For this species, tenerals were first trapped at BP the week of 22.VII. Tenerals comprised the majority of beetles trapped from 22.VII through 9.IX at BP, and from 22.VII through 16.IX at BM (Figure 1E). By October, emergence of new adults was nearly complete, though a small percentage of tenerals were captured 27.X.

The captures of *Calathus gregarius* adults throughout the year indicate that some adults overwinter along with the larvae. Thus, it appears the early season captures represent adults that have successfully overwintered, and these may mate a second year, as described by Gilbert (1956). However, the contribution of this portion of the population to the total reproductive potential appears minimal.

The capture results for the lebiine carabids show that *Dromius piceus* is exclusively arboreal. *Pinacodera platicollis* and *P. limbata* are active both on the ground and in the trees. *P. platicollis* overwinters as an adult in the leaf litter, with females more active on the ground in spring. This is apparently ovipositional activity, as the larvae are terrestrial (Mahar 1978). *P. limbata* overwinters on the ground principally in the larval stage, possibly with some adults also overwintering. Like *P. platicollis,* the larvae are terrestrial, and the activity of females on the ground is probably related to oviposition. The complete life histories for both *Pinacodera* spp. are given by Mahar (1978).

Analysis of Diversity

Three parameters of the floral composition at the study sites can be considered in relation to the diversity of the carabid fauna. These parameters are canopy closure, patchiness of distribution, and diversity. Increased closure of the canopy would reduce sunlight incident on the forest floor, and favor insects that require free moisture. Carabidae, with lightly sclerotized eggs, larvae, and pupae are such insects. Both BP and BM have a closed canopy, as exhibited by their high values of basal area/hectare (Table 1). Patchy distribution of plants would create a heterogeneous habitat, allowing diverse microenvironments to exist. Dublin and BM both show patchy plant distribution: Dublin with large between-tree distances; BM with a secondary canopy and moderate between-tree distances (Table 1). Heterogeneity at Dublin would not appear favorable for carabids, as the xeric lichen-covered openings would be unsuitable for larval development. At BM however, the mixing of dense secondary cover, closed primary canopy, and intermittent openings allows a diversity of microenvironments, all suitable for carabid habitation. The effects of the third parameter, diversity, are difficult to separate from those of patchy distribution; however an increase in plant species present offers some advantages patchy distribution can't. From a carabid viewpoint, one advantage would be an increased range of potential prey. This prey may be first order herbivores, or any insects that prosper due to increased food web complexity. Related to patchy plant distribution, a diverse flora can create many more different microenvironments due to patchy distribution than can a depauperate flora. A specific type of microenvironment could support species with a limited range of ecological requirements. The flora is most diverse at BM, least diverse at BP (Table 1).

On these criteria, we should expect Branch Mature to have the most di-

Table 7: Index of diversity, evenness, and dominance values for pitfall trap captures at the three study plots, based on number of individuals (Whittaker, 1972).*

Site	H'(s)	J	C
Dublin	1.573	.5654	.3069
Branch Pole	1.686	.5875	.2849
Branch Mature	1.826	.6232	.2128

* H' (s), J to base e.

verse carabid fauna. In fact, the diversity of the carabid fauna does increase in the upland oak forest as succession proceeds. The total number of species taken at the scrub oak plot at Dublin was only 18, but 24 species were taken in each of the closed stands (Table 3).

The Shannon-Weaver index of diversity was highest for the most mature stand (Table 7), though the differences were not statistically significant (Poole 1974). The evenness value showed a more equal abundance of species in the successionally more mature forest areas. Correspondingly, dominance was highest in the open plot, and decreased with succession. Thus, these measures of diversity and dominance point to an increase in the number of carabid species present, and a decrease in dominance, as succession proceeds in the upland oak forest.

The capacity of the successionally advanced site to support more competition can be related to its ability to support closely related species. At Branch Mature, *Pterostichus pensylvanicus* and *P. mutus, Myas coracinus* and *M. cyanescens,* and *Synuchus impunctatus* and *Calathus gregarius* were trapped in the most equal numbers. That these species pairs represent intense competition for resources is not conclusively proven. However, they possess similar life cycles within each pair; two pairs are of congeners, and the third is represented by closely related genera; and thus members of each pair would be expected to possess similar ecological requirements. *Pinacodera limbata* and *P. platicollis* are also closely related species which are abundant at BM; however, competition may be reduced due to temporal separation in life cycles.

As mentioned above, the availability of various types of microhabitats within a diverse stand can allow species with restricted ecological requirements to colonize portions of that stand. Thus, as a heterogeneous site is sampled, we would sample these subsections, and collect the various species restricted to specific microhabitats. This increase in species accounted for by sampling through a changing habitat is discussed by Hairston and Byers (1954), and is exemplified in the present study by the captures of *Episcopellus autumnalis.* With this species, almost all captures were restricted to two isolated areas at Branch Mature.

Grüm (1976) compared the species domination structure of carabids found at three sites of varying floral composition. He found that increased habitat heterogeneity resulted in decreased dominance in the carabid fauna. Allen and Thompson (1977) conjectured that most temperate forests contained carabid faunas that were dominated by relatively few species.

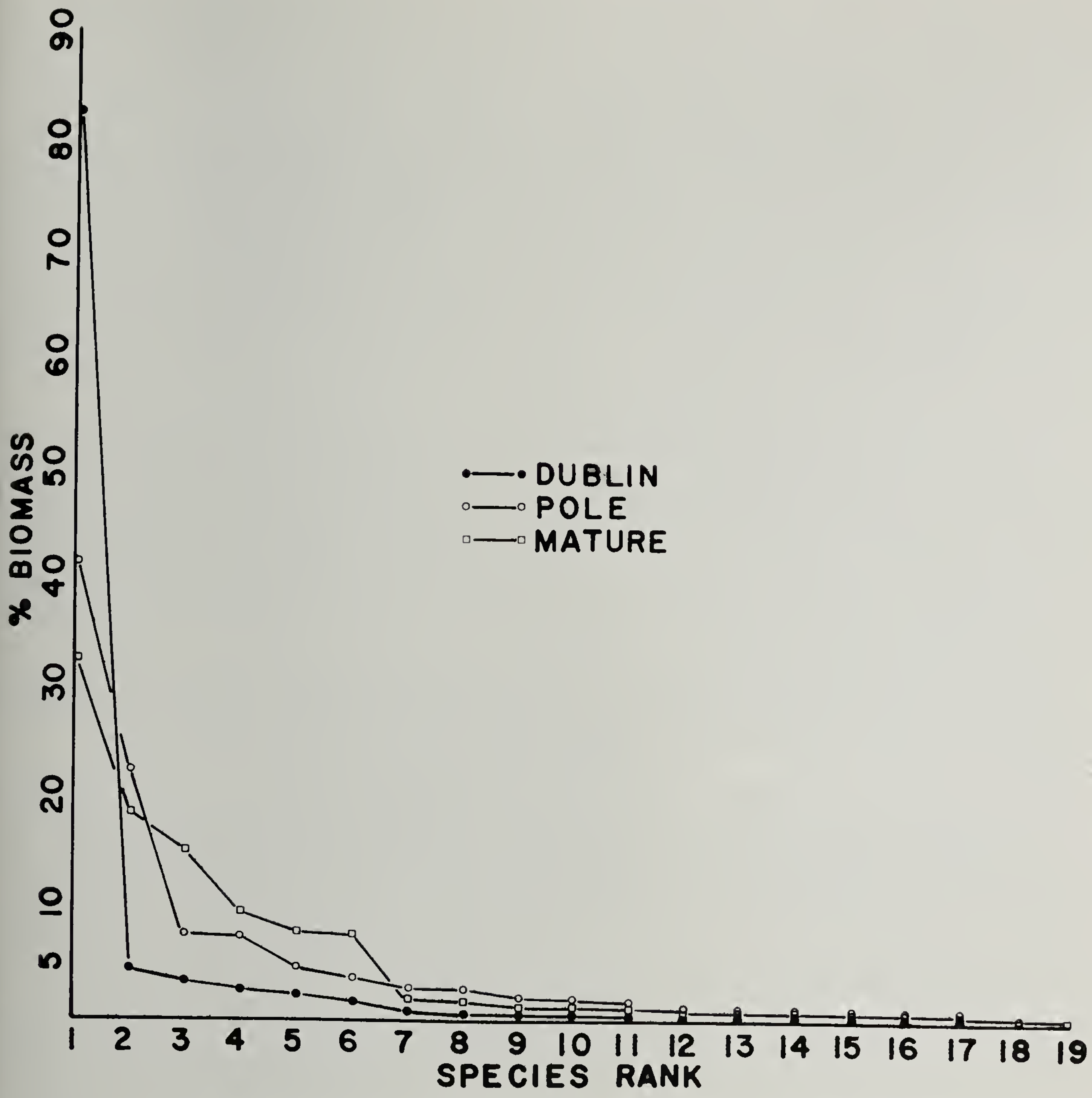

Figure 2, Dominance-diversity curve for percent contribution to total biomass for each species, versus species rank.

For the oak forest, an analysis of biomass contribution versus species rank for the species trapped by pitfall traps was made, and results indicated that the successionally more mature plots exhibited greater contribution to biomass from an increased number of species (Figure 2). Thus, whereas the scrub oak forest site exhibited the dominance-diversity structure of the geometric series or niche pre-emption model, the closed stands tend to exhibit curves more similar to the MacArthur, or random niche boundary model (Whittaker 1972). This comparison of the curve structure for the 3 habitats is simply another means by which the increased tolerance for competition, and species packing in the mature stands can be visualized.

Faunal Composition

Much of the foregoing analysis has been based on pitfall trap data. The best view of the community composition must be accomplished by studying all carabids present, and so pitfall trapping data has its limitations.

The use of sticky board traps produced perhaps the most significant results. The presence of a complex of arboreal lebiine carabids was discovered by this means. Whereas *Pinacodera* spp. use the trees for part of their life span, *Dromius piceus* appears to be exclusively arboreal. *Plochionus timidus* was also sampled by this method.

The other methods used also helped to discover rarer species in the plots. All of the specimens taken by means other than pitfall traps were winged (Table 4), and of these, 10 species had not been collected in pitfalls. For many, absence from pitfalls, strong flight ability, and what is known of biology suggest that they are colonists from sources outside the study plots. They may be overwintering adults, such as *Agonum tenue* or *Lebia bivittata,* or adults dispersing during the breeding season, such as *Dyschirius* sp. and *Lebia viridis.* Nonetheless, they represent a constant source of new propagules for suitable habitats within the forest.

A second, and the major component of the fauna, are those species that are resident in the forest, meaning that their progeny develop there. These residents vary from ubiquitous species having broad ecological requirements, to those that are very rare and found only in subsections of one habitat. Ubiquitous species include *Pterostichus pensylvanicus* and *Calathus gregarius,* both found in many types of eastern forest areas. Very rare residents include *Episcopellus autumnalis, Dicaelus purpuratus,* and *Cymindis neglecta* as examples. Another type of resident species is *Calosoma frigidum,* which has a very mobile adult stage, but which has larvae developing in the plots.

The range in variation of ecological requirements of the various species in the upland oak forest can be expected to be a continuum. Thus we should not expect certain species to be diagnostic of the forest type. As the area has been recently colonized, the species present now have been successful over a fairly short period of time. Continued stability in the area, coupled with floral succession should allow certain species to colonize the habitat, and conceivably outcompete present residents. To categorize the carabid fauna would be to mask its dynamic aspect, one that has allowed establishment of a relatively diverse fauna on what was barren soil less than a century ago.

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